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NOTES ON THE HARPACTICOID COPEPODS *ATTHEYELLA PILOSA* AND *A. CAROLINENSIS*, ASSOCIATES OF CRAYFISHES IN THE EASTERN UNITED STATES

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Among the North American freshwater copepods described by Chappuis are 2 species of the harpacticoid genus *Attheyella*. *A. pilosa* was described from Mammoth Cave, Kentucky, and Donnaldson Cave, Indiana (Chappuis, 1929a); *A. carolinensis* was described from Chapel Hill, North Carolina (Chappuis, 1932). An amplified description of *A. carolinensis* from the type locality was given by Coker (1934), and the species was later reported from Mountain Lake, Virginia (Carter, 1944) and, erroneously, from Doe Run, Kentucky (Prins, 1964). The only published report of *A. pilosa* since its discovery is a record of a single female from Luchil Cave, Yucatan (C. B. Wilson, 1936). The Yucatan specimen is not in the collections of the Smithsonian Institution, and a record so distant from the type-locality cannot be accepted without confirmation.

Reexamination of the Doe Run specimens, which Prins found on crayfishes, showed them to be *A. pilosa* rather than *A. carolinensis*. In an attempt to shed some light on the distribution of the 2 species and on the life history of *A. pilosa* we have examined harpacticoids found in association with crayfishes from a number of localities, mostly in the southeastern United States, including 22 samples from Doe Run. Since *A. pilosa* and *A. carolinensis* are similar in many respects and

since the original descriptions do not point out adequately the differences between the 2 species, we take this opportunity to redescribe and contrast their diagnostic characters.

Attheyella pilosa Chappuis
Figs. 1, 2, 3a–j

Attheyella (Brehmiella) pilosa Chappuis, 1929a, pp. 53–55, figs. 5–11; 1929b, p. 488 [in list]; p. 507 [in key]; 1931, pp. 348–351, figs. 5–11 [reprint of original description and figs.]; 1933, p. 19 [in list].—Lang, 1948, p. 984, fig. 3 [copied from Chappuis].
Attheyella (Ryloviella) pilosa Chappuis.—Borutsky, 1952, pp. 282–283 [p. 260 in 1964 translation], fig. 79: 4–6 [copied from Chappuis].
Attheyella pilosa Chappuis.—Pennak, 1953, p. 403 [listed in footnote]. —M. S. Wilson, 1956, p. [in list].—Barr, 1968, p. 159.
Attheyella (Mrazekiella) pilosa Chappuis.—M. S. Wilson and Yeatman, 1959, p. 847, fig. 29.201 [copied from Chappuis].
[?] *Attheyella pilosa* Chappuis.—C. B. Wilson, p. 79.
Attheyella carolinensis Chappuis.—Prins, 1964, pp. 370–371.

Female body length without caudal setae usually 0.58–0.70 mm (extremes measured: 0.53 and 0.76 mm). Male body length usually 0.52–0.64 mm (extremes measured 0.46 and 0.68 mm). Posterior margins of body segments serrate. Body clothed with minute spinules. Urosomites 2–5 with rows of slender spines anterior to serrate posterior margin, spine row sometimes incomplete middorsally on urosomite 5, spines and serrations interrupted ventrally by leg 6 on male urosomite 2. Anal operculum with numerous minute serrations. Caudal ramus conical, length about 3 times width of distal margin, dorsal ridge well developed, dorsal spine inserted at about proximal third of ramus, medial margin with row of fine setae, lateral part of dorsal surface with delicate spines, more numerous in male. Middle caudal seta about ½ length of body. Nuchal organ oval. Genital field as in fig. 1f; leg 6 a single seta.

Female 1st antenna 7-merous, rarely 8-merous when long distal segment divided by suture; 1st segment with curved row of fine spinules on dorsal surface and curved row of larger spinules on ventral surface; esthete of 4th segment reaching just beyond apex of appendage; all segments except 4th and 5th with a single sparsely plumose seta on anterior margin. Male 1st antennae with moderately enlarged 4th segment.

2nd antenna with 1-merous exopod bearing 4 setae and 2 surface spines. Mandible with 1-merous palp 1 bearing 4 setae; gnathal lobe armed from ventral to dorsal with a robust bicuspid tooth, a slightly less robust tricuspid tooth, several smaller teeth with sharp cusps, and a dorsal seta. Proximal lobe (precoxa) of 1st maxilla bearing 9 spines; middle lobe (coxa) with a single spine; distal lobe with 7 spines.

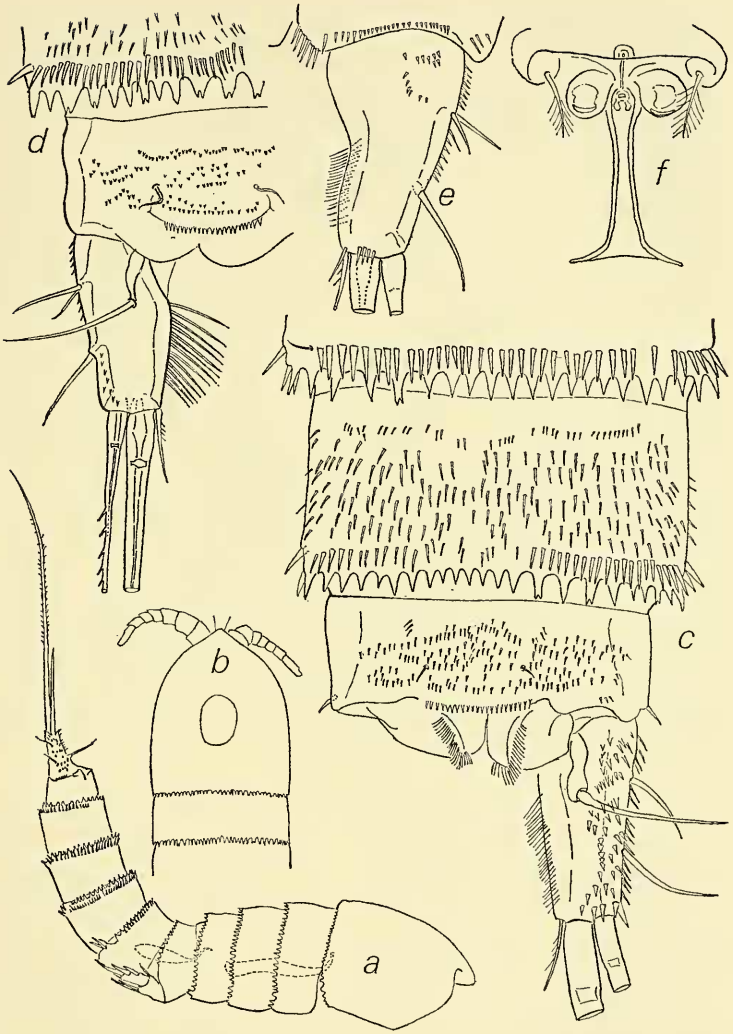

FIG. 1. *Attheyella pilosa* Chappuis: a, male, lateral; b, anterior end of female, dorsal; c, posterior urosome of male, dorsal; d, posterior urosome of female, dorsal; e, female caudal ramus, ventral; f, genital field.

Proximal lobe of 2nd maxilla with 2 setae, one with recurved tip bearing long setules; 2nd lobe with 3 setae, 2 of them similar to those of proximal lobe; endopod with strong terminal spine flanked by 2 setae, endite bearing 3 setae. 1st segment with proximal seta, anterior margin serrate. Sternal plate inconspicuous, with smooth margin. Leg 1, exopod shorter than 1st segment of endopod; 3rd segment of endopod shorter than that of *A. carolinensis*. Legs 2–4 like those of *A. carolinensis*; endopod of male leg 2 without subterminal lateral spine or 2nd segment; leg 3 endopod 2-merous in female, 3-merous in male, medial process of 2nd segment doubly curved with minute terminal barb; 2nd segment of leg 4 endopod usually with 4 setae in addition to subterminal spine, occasionally with 5 setae. Female leg 5 with low basal expansion of proximal segment bearing 5 setae of which most lateral is by far the shortest; distal segment less than twice as long as wide, with rows of surface spines and 5 marginal setae, medial seta only slightly longer than longest distal seta. Male leg 5 with 2 setae on basal expansion, lateral half as long as medial, sometimes absent. Leg 6 a low plate with 2 strong pinnate setae and a slender plumose outer seta.

Relationships: Of the 9 species of *Attheyella* known from North America (according to Wilson and Yeatman, 1959), only *A. americana* (Herrick), *A. carolinensis* Chappuis, *A. illinoisensis* (S. A. Forbes), *A. obatogamensis* (Willey), and *A. pilosa* have been found in the United States east of the Mississippi River. Three of these species are readily distinguishable from *A. pilosa*. In *A. americana* and *A. illinoisensis* the caudal ramus is short, about as wide as long, and in *A. obatogamensis* the female caudal ramus has a prominent spiniform process on the medial margin. *A. carolinensis*, however, closely resembles *A. pilosa*, but can be distinguished from it as follows:

A. pilosa

1. Caudal ramus narrower, with comb of fine setae along medial margin and from few to many minute triangular spines on dorsal surface.
2. Spine row anterior to serrate margin of urosomites complete dorsally (may be incomplete in ♀ urosomite 5).
3. 3rd segment of endopod of leg 1 shorter.
4. Basal expansion of ♀ leg 5 with 5 setae.
5. Distal segment of ♀ leg 5 short and wide, about 1.7 times as long as wide; longest seta only slightly longer than medial seta.

A. carolinensis

1. Caudal ramus broader, without setal comb on inner margin, with spiniform setae on lateral margin and in row extending posteriad from dorsal seta.
2. Spine row limited to ventral and lateral parts of urosomites.
3. 3rd segment of endopod of leg 1 longer.
4. Basal expansion of ♀ leg 5 with 4 setae.
5. Distal segment of ♀ leg 5 longer and narrower, about 2.6 times as long as wide; longest seta more than twice as long as medial seta.

Fig. 2. *Attheyella pilosa* Chappuis: a, antenna 1, female; b, antenna 1, male; c, antenna 2, male; d, gnathal lobe of mandible, female; e, maxilla 1, female; f, maxilla 2, female; g, maxilliped, male.

A more detailed comparison than we have made would undoubtedly reveal other differences, but those listed above were most obvious to us. In practice we have found contrasting items 2 and 5 most useful, since the ornamentation of the caudal ramus (item 1) is often obscured by adhering particles of detritus. The spine rows of the urosomites are easily seen in specimens cleared in glycerine or lactic acid, and the relative lengths of the setae of the distal segment of leg 5 are usually visible in undissected specimens viewed laterally.

Localities of specimens examined (major drainage systems listed in parentheses). VIRGINIA.—Giles Co.: Sinking Creek, Newport (New River), H. H. Hobbs, Jr. Smyth Co.: Middle Fork, Holston River (Tennessee R.), 2.5 mi. E of Marion, R. D. Ross. White Oak Branch, just above confluence with North Fork of Holston River, Chatham Hill (Tennessee R.), W. Harman & H. H. Hobbs, Jr. SOUTH CAROLINA.—Greenville Co.: In pools of cascading stream about 7 mi. W of Cleveland on US 276, (Saluda R.), H. H. Hobbs, Jr. GEORGIA.—Catoosa Co.: Tributary to Chicamauga Creek crossing Ga. 2 4.1 mi. W of junction of Ga. 71 and Ga. 2 (Tennessee R.), H. H. Hobbs, Jr. Catoosa Springs, 2 mi. E of Ringgold (Tennessee R.), S. Peck, A. Fiske. Chatooga Co.: Blowing Springs Cave, 2.5 mi. E of Cloudland (Tennessee R.), J. R. Holsinger. Floyd Co.: Stream about 5 mi. W of Rome on Ga. 20 (Coosa R.), H. H. Hobbs, Jr. Stream 2 mi. W of Junction of Ga. 100 N and Ga. 20 on Ga. 20 (Coosa R.), H. H. Hobbs, Jr. Polk Co.: Tributary to Cedar Creek at northern city limits of Cedartown on Ga. 100 (Coosa R.), H. H. Hobbs, Jr. TENNESSEE.—Unicoi Co.: Erwin Highway, Buffalo Creek; Erwin Fish Hatchery (both Tennessee R.); P. C. Holt and class. Jackson Co.: Roaring River, 8–9 mi. above mouth (Cumberland R.). KENTUCKY.—Hardin Co.: Nelson Cave (Ohio R.), T. C. Barr. Edmonson Co.: Mammoth Cave (Ohio R. via Green R.), Chappuis (1929a). Hart Co.: Cub Run Cave (Ohio R. via Green R.), Barr (1968). Meade Co.: Doe Run (Ohio R.), R. Prins. INDIANA.—Lawrence Co.: Donnaldson Cave (Wabash R.), Chappuis (1929a). ILLINOIS.—Ogle Co.: Kilbuck Creek, 16.4 mi. W of Kingston (Mississippi R.), P. C. Holt.

Attheyella carolinensis Chappuis
Fig. 3k–l

Attheyella (Brehmiella) carolinensis Chappuis, 1932, pp. 226–229, figs. 1–10.—Lang, 1948, pp. 985–986, fig. 392.1 [copied from Chappuis and from Coker].

Attheyella carolinensis Chappuis.—Coker, 1934, pp. 116–118, pls. 10–11.—Carter, 1944, p. 158.—Pennak, 1953, p. 407, figs. 256C [from Coker].

Attheyella (Ryloviella) carolinensis Chappuis.—Borutsky, 1952, p. 283 [p. 261 in 1964 translation], fig. 79: 7–9 [copied from Coker].

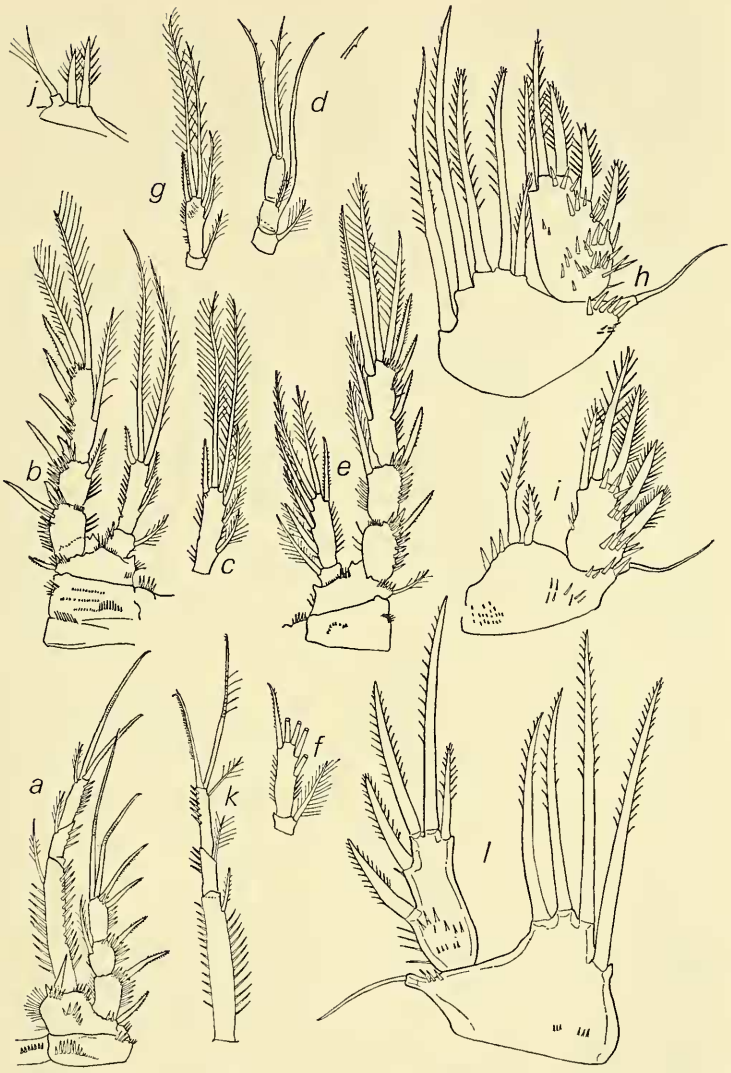

FIG. 3. *Attheyella pilosa* Chappuis: a, leg 1, female; b, leg 2, female; c, leg 3, female, distal segment of endopod; d, leg 3, male, endopod; e, leg 4, female; f, leg 4, endopod, from another female; g, leg 4, male, endopod; h, leg 5, female; i, leg 5, male; j, leg 6, male. *Attheyella carolinensis* Chappuis: k, leg 1, female, endopod; l, leg 5, female.

Attheyella (Mrazekiella) carolinensis Chappuis.—M. S. Wilson and Yeatman, 1959, p. 847, fig. 29.200 [copied from Coker].

Coker (1934) has provided a well illustrated account of this species, but a few points should be clarified. In Coker's account of the head appendages the 1st antenna is called "antenna" and the 2nd antenna is called "antennnule." His drawing of leg 1 (pl. 11, fig. 1) omits the row of setae along the medial margin of the 1st segment of the endopod. A nuchal organ identical in appearance to that of *A. pilosa* is present altho not illustrated by Coker.

Localities of specimens examined (major drainage systems listed in parentheses). WEST VIRGINIA.—Greenbriar Co.: Fuller's Cave, 37°56′00″N, 80°25′38″W, Paul J. Starr. VIRGINIA.—Mountain Lake (county and drainage system uncertain), Marjorie E. Carter (1944). Carrol Co.: Stream flowing S from plateau 10 mi. S of Hillsville on US 221, elevation 3000 ft. (Ohio R. via New River), H. H. Hobbs, Jr. Smyth Co.: McHenry Creek off Va. 91, Saltville (Tennessee R. via Holston R.), J. R. Cunningham. NORTH CAROLINA.—Orange Co.: Chapel Hill (Cape Fear R.), R. E. Coker (1934). Transylvania Co.: Thompson River headwaters, 1.1 mi. N of Bohaynee Church (Savannah R. via Keowee R.), R. Prins. Jackson Co.: Whitewater River, off NC 107 (Keowee R.), R. Prins. Tributary from Fairfield Lake off US 64 (Keowee R.), R. Prins et al. East Fork Chatooga River at N.C.-S.C. state line off N.C. 107 ("old" Tugaloo R.), R. Prins et al. SOUTH CAROLINA.—Pickens Co.: Tributary to Oolenoy River, 0.3 mi. E of SC 11 off US 69 (Saluda R.), R. Prins, G. E. Dillard. Greenville Co.: About 7 mi. W of Cleveland on US 76 in pools of cascading stream (Saluda R.), H. H. Hobbs, Jr. South Saluda River at boundary of Pickens and Greenville Cos. on SC 11 (Saluda R.), H. H. Hobbs, Jr. Oconee Co.: Chauga River at Cassidy Bridge on SC 290 ("old" Tugaloo R.), R. Prins, J. R. Cunningham, V. H. McCaskill. Mud Creek at SC 172 (Little R.), R. M. Shealy. Ramsey Creek at Chauga River on US 76, about 5 mi. W of Westminster (Savannah R.), H. H. Hobbs, Jr. Small stream between Long Creek and Chatooga R. on US 76 Chatooga R.), H. H. Hobbs, Jr. GEORGIA.—Rabun Co.: Timpson Creek, about 6 mi. W of Clayton, on US 76 (Savannah R.), H. H. Hobbs, Jr. Small tributary to Chatooga River immediately W of crossing on US 76 (Chatooga R.), H. H. Hobbs, Jr. Towns Co.: Stream at junction of Ga. 17 and Ga. 66, 12 mi. S of Hiawassee (Hiwassee R.), H. H. Hobbs, Jr. Stream at northern city limits of Young Harris (Hiwassee R.), H. H. Hobbs, Jr. Union Co.: 1.7 mi. NE of Blairsville on US 76 (Hiwassee R.), H. H. Hobbs, Jr. Fannin Co.: Small stream 3 mi. N of Blue Ridge on Ga. 5 (Hiwassee R.), H. H. Hobbs, Jr. 7 mi. S of Morganton on Ga. 60, seepage area and mountain spring (Hiwassee R.), H. H. Hobbs, Jr. Gilmer Co.: Hells Creek, running into Carter's Reservoir (Cooawattee R.), H. H. Hobbs, Jr. Pickens Co.: Tributary to Talking Rock Creek, 1.7 mi. E of boundary of

FIG. 4. Distribution records of *Attheyella pilosa* (stars) and *A. carolinensis* (triangles). Some records in Georgia are omitted because of the scale; these are shown in fig. 5.

Pickens and Fannin Cos. on Ga. 156 (Coosawattee R.), H. H. Hobbs, Jr. KENTUCKY.—Bell Co.: Mill Creek, near Pineville (Cumberland R.), Donald L. Batch.

DISTRIBUTION OF *ATTHEYELLA PILOSA* AND *A. CAROLINENSIS*

Locality records for the two harpacticoid species are shown in figure 4. All records except the type-localities are from collections that we have examined. In only one instance did both species occur in a single

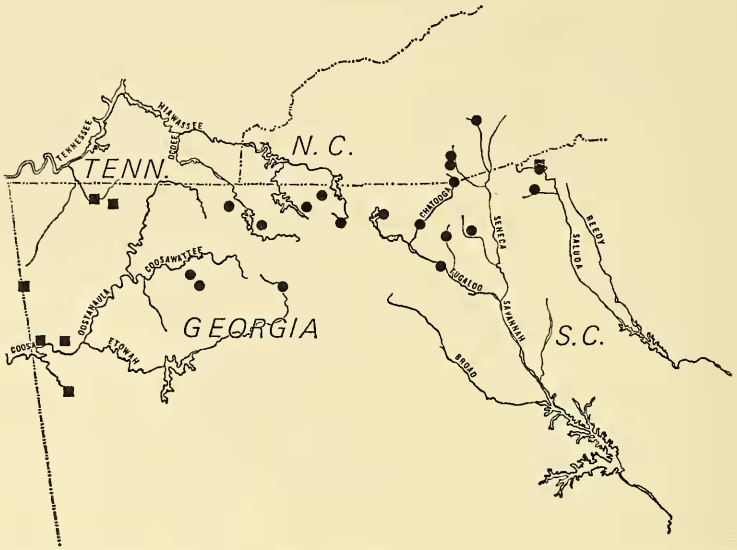

FIG. 5. Distribution records of *Attheyella pilosa* (squares) and *A. carolinensis* (circles) in northern Georgia and parts of adjacent states.

collection; this was from a stream belonging to the Saluda River drainage system near Cleveland, Greenville Co., S. C. The associated crayfishes were *Cambarus asperimanus* and an undescribed species of *Cambarus* belonging to the *C. bartonii* group. Our records are far too inadequate to support any detailed generalizations concerning the distribution patterns, but the preponderance of *A. pilosa* west of the Appalachians and of *A. carolinensis* in the drainage systems of streams flowing into the Atlantic is obvious. The area for which we have the most detailed information on the occurrence of the two species is in northern Georgia and northwestern South Carolina, where collections of crayfishes have been obtained by H. H. Hobbs, Jr. and by R. Prins. Figure 5 shows the distribution of the two species in this region and some of the principal tributaries of the major drainage systems. Besides occurring in the upper drainage systems of the Savannah and Saluda Rivers, *A. carolinensis* is present in streams leading to the Tennessee and Coosa Rivers. Progressing down-stream in the drainage of the Coosa, and perhaps in that of the Tennessee, *A. carolinensis* is replaced by *A. pilosa*.

The record of *A. carolinensis* is southeastern Kentucky (Mill Creek, Cumberland River drainage, near Pineville, from *Cambarus distans*) upsets the otherwise rather neat east-west separation of the two species. The limits of drainage systems, however, do not necessarily impose barriers to their movements. Some species of crayfishes are known to

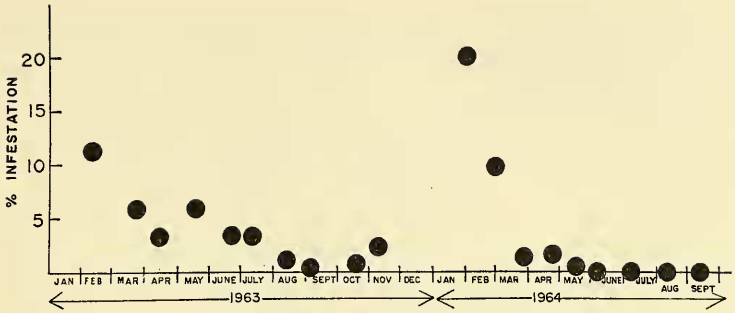

FIG. 6. Incidence of infestation of *Orconectes r. rusticus* with *Attheyella pilosa* at Doe Run, Kentucky.

migrate over land during damp weather, presumably carrying their associates with them. Moreover, migration between stream systems thru underground connections is a likely possibility for the two harpacticoids. The type-locality of *A. pilosa* is subterranean, and both species are inhabitants of spring-fed streams. Finally, the role of stream piracy on distribution cannot be overlooked. It really is not surprising that the distribution patterns of the two species do not coincide exactly with those of drainage systems.

THE BIOLOGY OF *ATTHEYELLA PILOSA* AT DOE RUN

As reported by Prins (1964), *A. pilosa* (called *A. carolinensis* by Prins) was collected at Doe Run in "dense reddish assemblages from the pleopods, the bases of the coxae of the pereiopods, the hairs around the sterna, and various other places on the under-surfaces of *Cambarus tenebrosus* Hay . . . and *Orconectes rusticus rusticus* (Girard)." Between November 1962 and September 1964 Prins collected 22 samples from 3 collecting sites on Doe Run: Station I, at the source of the stream; Station IA, ¼ mile downstream, and Station II, 2 miles downstream (Minckley, 1963). These collections, which were made during every month except October and December, have been studied in an attempt to obtain information on the life history of *A. pilosa.* From each sample a number of specimens (between 50 and 160) were selected randomly. For each specimen selected the sex and developmental stage were determined, and the total length (tip of rostrum to end of caudal rami) was measured.

Seasonal occurrence: Of the crayfish hosts, only *Cambarus* occurred at stations I and IA; both *Cambarus* and *Orconectes* occurred at station II. The incidence of infestation was usually much higher in *Cambarus,* perhaps because of their habit of spending more time in burrows in the banks and on the channel bottom where they may be more accessible

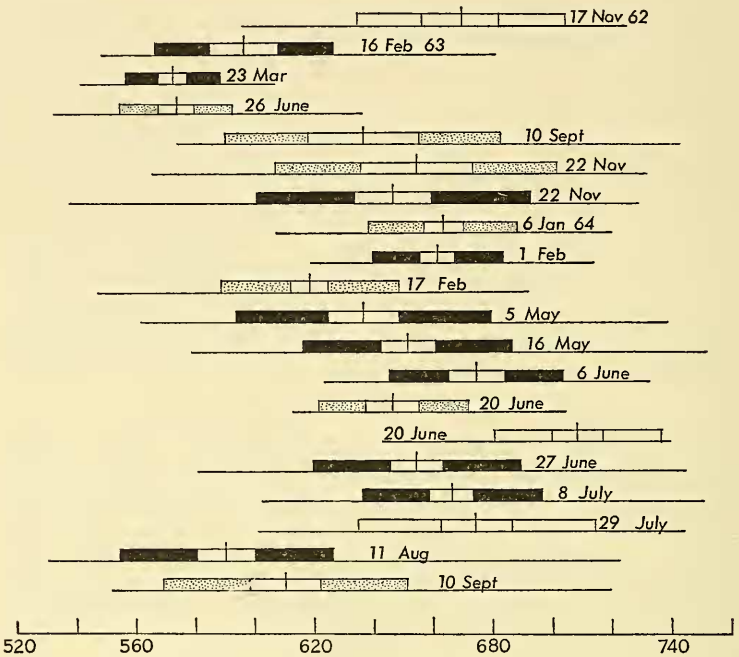

FIG. 7. Variation in length of *Attheyella pilosa* populations at Doe Run, Kentucky. For each diagram the horizontal line represents the sample range, the central vertical line the sample mean, the inner white rectangles the value of 2 standard errors; the distance from the mean to the edge of an outer rectangle equals the value of 1 standard deviation. Stations indicated by outer rectangle: station I—white, station IA—stippled, station II—black.

to the copepods. Seasonal variations in the incidence of infestation of *Cambarus*, which molts thruout the year in Doe Run, were very erratic. On the other hand, infestation of *Orconectes* is greatest in the winter when it is torpid and rarely molts, and least in midsummer when molting is most frequent (fig. 6). This suggests that *Attheyella* as has been suggested for branchiobdellid worms (Hobbs, Holt, and Walton, 1967, p. 13) does not return to the host when the old exoskeleton is shed in molting. In contrast, Hobbs, Holt, and Walton (1967, p. 12) report that after a molt the entocytherid ostracods leave the host's recently molted skeleton and make their way to the new one.

Only adult males and females of *Attheyella* were found, in spite of a careful search for copepodids. Immature specimens must be free-living on the stream bottom. In the harpacticoid *Nitocrella divaricata* (Chap-

puis), which lives in the gill chamber and on the body surface of the European crayfish *Astacus astacus* (L.), both copepodids and adults are found on the host; only the nauplii are free-living (Chappuis, 1927). At present we do not know to what extent association with a crayfish host is mandatory for *A. pilosa*, since a systematic search has not been made for free-living specimens in Doe Run.

Females with egg sacs were found in samples collected during February, March, April, June, and September. Breeding probably occurs thruout the year.

Sex ratio: In most samples the numbers of males and females were nearly equal. The percentage of males varied from 25 (5 May 1964) to 65 (22 Nov. 1964, sta. IA). We feel that these fluctuations are fortuitous rather than indicative of significant variations in the sex ratio. The percentage of males in all samples combined was 49.8.

Population structure: Size-frequency histograms were constructed for all samples in an attempt to identify the generations comprising the populations and to trace their emergence and decline from month to month. The composition of the samples proved to be so complex that the desired information could not be extracted with any confidence. The histograms had from 2 to several peaks, not all clearly defined, and it usually was not possible to correlate the peaks of one sample with those of another.

Such a picture is to be expected from a multivoltine species that breeds during most or all of the year and has a short period between generations (probably not more than 1 or 2 months). This results in several generations, perhaps 5–10 during a year. The size composition of one generation may differ from that of another generation in the same local population, and the size composition also may be different in comparable generations from different local populations. As it moves about, a crayfish may encounter and be infested by several different local populations of *Attheyella*. Thus the harpacticoid assemblages on a crayfish may be so heterogeneous that it is extremely difficult to identify the component populations.

Fig. 7 shows the seasonal variation in length of *A. pilosa* at the 3 stations. We can offer no explanation for the fluctuations other than the heterogeneity of the samples. The statistical variability of the samples does not seem excessive; the coefficient of variability ranged from 2.4 to 8.4, but usually lay between 3 and 6. We could find no relationship between size and water temperature; this is not surprising since the annual range in temperature in the cool, spring-fed Doe Run was slight: Station I, 2.6°C, Station IA, 4°C, and Station II, about 8°C.

Acknowledgments

Many of the harpacticoids were sorted for us from crayfishes by Margaret Walton at the request of Horton H. Hobbs, Jr., who collected them. We are grateful to Dr. Hobbs for his cooperation and to Miss

Walton for patiently undertaking this tedious task. Field work at Doe Run by Prins was supported in part by U. S. Atomic Energy Commission under contract No. AT-(40-1)-2595 with the University of Louisville, Louisville, Kentucky. For critical reviews of the manuscript we are grateful to Drs. Gerald C. Cole, John R. Holsinger, and Perry C. Holt.

Literature Cited

Barr, Thomas C., Jr. 1968. Ecological studies in the Mammoth Cave system of Kentucky. Intern. J. Speleology 3(1 + 2): 147–204, pls. 37–64.

Borutsky, E. V. 1952. Crustacea, vol. 3, no. 4, Freshwater Harpacticoida. Fauna SSSR, Zool. Inst. Akad. Nauk SSSR, N.S., no. 50, 424 pp. [English translation by Israel Program for Scientific Translations, 396 pp., published in 1964].

Carter, Marjorie E. 1944. Harpacticoid copepods of the region of Mountain Lake, Virginia (with description of *Moraria virginiana* n. sp.). J. Elisha Mitchell Sci. Soc., vol. 60, no. 2, pp. 158–166, pls. 65–67.

Chappuis, P. A. 1927. Harpacticiden aus der Kiemenhohle des Flusskrebses. Archiv fur Hydrobiologie, vol. 17, no. 3, pp. 515–520.

———. 1929a. Copépodes cavernicoles de l'Amérique du Nord. (note préliminaire). Bull. Soc. Stiinte Cluj (Romania), vol. 4, pt. 2, pp. 51–57.

———. 1929b. Die Unterfamilie der Canthocamptinae. Archiv fur Hydrobiologie, vol. 20, pp. 471–516.

———. 1931. Biospeologica no. 16, Campagne spéologique de C. Bolivar et R. Jeannel dans l'Amérique du Nord (1928). 4, Crustacés Copépodes. Arch. Zool. Expér. Gén., vol. 71, no. 3, pp. 345–360.

———. 1932. Eine neue *Attheyella* aus Nordamerika. *Attheyella* (*Brehmiella*) *carolinensis* n. sp. Zool. Anz., vol. 98, nos. 7/8, pp. 226–229.

———. 1933. Biospeologica no. 59, Copépodes (première série), avec l'énumération de tous les Copépodes cavernicoles connus en 1930. Arch. Zool. Expér. Gén., vol. 76, no. 1, pp. 1–57.

Coker, Robert E. 1934. Contribution to knowledge of North American freshwater harpacticoid copepod Crustacea. J. Elisha Mitchell Sci. Soc., vol. 50, no. 1–2, pp. 75–141, pls. 1–15.

Hobbs, Horton H., Jr., Holt, Perry C., and Walton, Margaret. 1967. The crayfishes and their epizootic ostracod and branchiobdellid associates of the Mountain Lake, Virginia, region. Proc. U. S. Nat. Mus., vol. 123, no. 3602, pp. 1–84.

Lang, Karl. 1948. Monographie der Harpacticiden. Stockholm, vol. 1, pp. 1–896, figs. 1–361; vol. 2, pp. 897–1682, figs. 362–607, maps 1–378.

Minckley, W. L. 1963. Studies of the biology of a spring stream. Doe Run, Meade County, Kentucky. Wildlife Mongr., No. 11, pp. 1–124.

Pennak, Robert W. 1953. Fresh-water invertebrates of the United States. 769 pp., Ronald Press, New York.

Prins, Rudolph. 1964. *Attheyella carolinensis* Chappuis (Copepoda; Harpacticoida) on freshwater crayfishes from Kentucky. Trans. American Microscop. Soc., vol. 83, no. 3, pp. 370–371.

————. In press. Comparative ecology of the crayfishes *Orconectes rusticus rusticus* and *Cambarus tenebrosus* in Doe Run, Meade County, Kentucky. Intern. Rev. Ges. Hydrobiol.

Wilson, Charles B. 1936. Copepods from the cenotes and caves of the Yucatan Peninsula, with notes on cladocerans. Carnegie Inst. Washington Publ. no. 457, pp. 77–88.

Wilson, Mildred S. 1956. North American harpacticoid copepods. 1. Comments on the known freshwater species of the Canthocamptidae. 2. *Cantocamptus oregonensis* n. sp. from Oregon and California. Trans. American Microscop. Soc., vol. 75, no. 3, pp. 290–307.

Wilson, Mildred S., and Harry C. Yeatman. 1959. Free-living Copepoda, pp. 735–861. *In* W. T. Edmondson (ed.), Ward and Whipple's freshwater biology, 1248 pp., John Wiley & Sons, New York.